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Flower power: tree flowering phenology as a settlement cue for migrating birds

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Summary

1. Neotropical migrant birds show a clear preference for stopover habitats with ample food supplies; yet, the proximate cues underlying these decisions remain unclear.

2. For insectivorous migrants, cues associated with vegetative phenology (e.g. flowering, leaf flush, and leaf loss) may reliably predict the availability of herbivorous arthropods. Here we examined whether migrants use the phenology of five tree species to choose stopover locations, and whether phenology accurately predicts food availability.

3. Using a combination of experimental and observational evidence, we show migrant populations closely track tree phenology, particularly the flowering phenology of honey mesquite (*Prosopis glandulosa*), and preferentially forage in trees with more flowers. Furthermore, the flowering phenology of honey mesquite reliably predicts overall arthropod abundance as well as the arthropods preferred by migrants for food.

4. Together, these results suggest that honey mesquite flowering phenology is an important cue used by migrants to assess food availability quickly and reliably, while in transit during spring migration.

Key-words: foraging, habitat selection, migration, phenology, stopover

Introduction

Migration is an energetically demanding period in the annual cycle of many species of birds, and can impose strong selection on individuals and represent an important limitation to population viability (Lindström 1989; Marra, Hobson & Holmes 1998; Sillet & Holmes 2002; Heglund & Skagen 2005; Lind & Cresswell 2006; Newton 2006). Because of their small size and long-distance migration, Neotropical migrant songbirds are unable to carry sufficient energy reserves to migrate nonstop and must select habitats en route to stop and refuel (Moore & Aborn 2000). Stopover site selection directly influences survival and has cascading effects on future reproduction (Piersma 1990; Moore *et al.* 1995; Moore, Smith & Sandberg 2005); yet during migration, most individuals are in unfamiliar surroundings and have limited time and energy to sample habitats (Hutto 1985a; Loria & Moore 1990; Moore, Kerlinger & Simons 1990; Moore & Yong 1991; Moore & Aborn 2000; Petit 2000). Food limitation, predation, competition, and unfavourable weather all represent important costs associated with selecting stopover locations (Moore *et al.* 1995, 2005; Petit 2000) and theory would predict that birds should choose locations that minimize these costs (Fretwell & Lucas 1970; Fretwell 1972; Houston 1998). However, despite clear evidence that migrants exhibit habitat preference during stopover (Hutto 1985a; Moore *et al.* 1995, 2005), we know little about the ecological cues individuals use to select stopover locations (Petit 2000).

Variation in food resources, for example, can profoundly affect risk of starvation, exposure to predation, breeding energy budgets, and timing of breeding (Lima & Dill 1990; Piersma 1990; Moore *et al.* 1995, 2005; Newton 2006). Birds clearly prefer habitats that maximize the availability of food resources (Hutto 1985a; Moore *et al.* 1995), yet the cues that birds use to select these habitats remain largely unknown. Although direct sampling of food availability is the most accurate method of determining habitat suitability, the time and energy constraints migrants face may limit them to using vegetative and structural cues (Moore & Aborn 2000). Available foliage is generally correlated with the diversity and abundance of herbivorous insects (Marques, Price & Cobb 2000; Murakami, Hirao & Ichie 2007); therefore, changes in tree phenology (e.g. flowering, leaf flush, and leaf loss) may present insectivorous migrant birds with structural cues that reliably predict food availability.

Here we used observational and experimental evidence to examine whether insectivorous Neotropical migrant birds use tree phenology to choose stopover locations and if phenology accurately predicts food availability. Specifically, we asked: (i) Are macrohabitat patterns of avian diversity and abundance

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Table 1. Study species and sample sizes

	Family	Name		Code*	Count†	Forage‡	Arthropod§
		Scientific	Common				
Bird Species	Tyrannidae	*Tyrannus verticalis*	Western kingbird	WEKI	141	–	–
		Myiarchus cinerascens	Ash-throated flycatcher	ATFL	334	1	–
		Empidonax wrightii	Gray flycatcher	GRFL	14	–	–
		Empidonax difficilis	Pacific-slope flycatcher	PSFL	83	1	10
		Empidonax occidentalis	Cordilleran flycatcher	COFL			
	Regulidae	*Regulus calendula*	Ruby-crowned kinglet	RCKI	176	2	–
	Turdidae	*Turdus migratorius*	American robin	AMRO	61	–	–
		Catharus guttatus	Hermit thrush	HETH	11	–	–
		Catharus ustulatus	Swainson's thrush	SWTH	4	–	–
	Vireonidae	*Vireo plumbeus*	Plumbeous vireo	PLVI	10	–	–
		Vireo gilvus	Warbling vireo	WAVI	48	20	3
		Vireo bellii	Bell's vireo	BEVI	170	2	–
	Parulidae	*Vermivora ruficapilla*	Nashville warbler	NAWA	72	55	13
		Vermivora celata	Orange-crowned warbler	OCWA	159	92	14
		Wilsonia pusilla	Wilson's warbler	WIWA	200	122	26
		Dendroica nigrescens	Black-throated grey warbler	BTYW	43	28	2
		Vermivora luciae	Lucy' warbler	LUWA	412	16	–
		Oporornis Philadelphia	MacGillivary's warbler	MGWA	29	8	5
		Dendroica townsendi	Townsend's warbler	TOWA	34	24	5
		Dendroica occidentalis	Hermit warbler	HEWA	15	10	–
		Dendroica petechia	Yellow warbler	YWAR	230	6	2
		Dendroica coronata	Yellow-rumped warbler	YRWA	547	76	3
		Geothlypis trichas	Common yellowthroat	COYE	340	–	–
		Ictera virens	Yellow-breasted chat	YBCH	219	1	–
	Oriolidae	*Icterus bullockii*	Bullock's oriole	BUOR	188	–	–
	Thraupidae	*Piranga ludoviciana*	Western tanager	WETA	45	–	–
		Piranga rubra	Summer tanager	SUTA	23	–	–
	Cardinalidae	*Passerina amoena*	Lazuli bunting	LABU	14	–	–
Tree Species	Salicaceae	*Populous fremontii*	Fremont cottonwood	FRCO	7700	–	59
		Salix goodingii	Gooding's willow	GOWI	4200	–	59
	Fabaceae	*Prosopis pubescens*	Screwbean mesquite	SCME	7800	–	60
		Prosopis glandulosa	Honey mesquite	HOME	7800	–	71
	Tamaricaceae	*Tamarix sp.*	Tamarisk	TAMA	7500	–	60

*Species codes used for labels in all figures are based on common names following the American Ornithological Union. Columns denote sample sizes for point counts and tree phenology†, avian behavioural observations‡, and lavage and tree insect sampling§.

correlated with seasonal variation in tree phenology? (ii) Do migrant birds prefer particular phenological cues when selecting foraging microhabitats? and (iii) Do these cues accurately predict food availability?

Methods

STUDY SYTEM AND SPECIES

We examined the role of tree phenology in avian habitat selection between March and May of 2001 to 2004 at Cibola National Wildlife Refuge along the lower Colorado River. We established a study site along the riparian corridor, dominated by five tree species (40% FRCO, 25% HOME, 17% SCME, 7% GOWI, 11% TAMA) and seasonally occupied by > 100 species of migrant birds of which we focused on 28 species of insectivorous Neotropical migrant songbirds (Table 1).

MACROHABITAT PREFERENCE

To assess the ability of the avian community to use tree phenology as a settlement cue, we established two 1-km transects through the middle of the study area, separated by 300 m. Transects did not differ in vegetation and here are not considered independent samples, but rather a means of assuring overlap between estimates of avian abundance and stand phenology. Each week, the same observer walked both transects visually sampling 100 trees of each species found within 50 m. At each tree, we calculated phenology by visualizing a full crown and estimating the proportion of the tree currently covered by leaves, flowers, and fruits. We then averaged data for each species to obtain weekly stand conditions (after van Riper 1980). To increase rigor, we also documented phenology using a digital camera, but since both methods produced similar results ($t_{50} = 14{\cdot}38$, $P = 0{\cdot}17$), we present the larger samples based on visual estimates. Simultaneously, we conducted 25-m fixed-radius point counts (Hutto, Pletschet & Hendricks 1986) from sunrise to 09.00 h at eight points along each transect. To minimize bias, we reversed starting points for avian counts and tree phenology weekly. We tested for correlations between phenology and raw estimates of avian diversity and abundance using a combination of Pearson correlations and general linear models (GLM) that included migrant species, year, and transect as factors and date as a covariate. We excluded nonsignificant interactions from trial models and corrected for multiple tests using a Bonferroni correction.

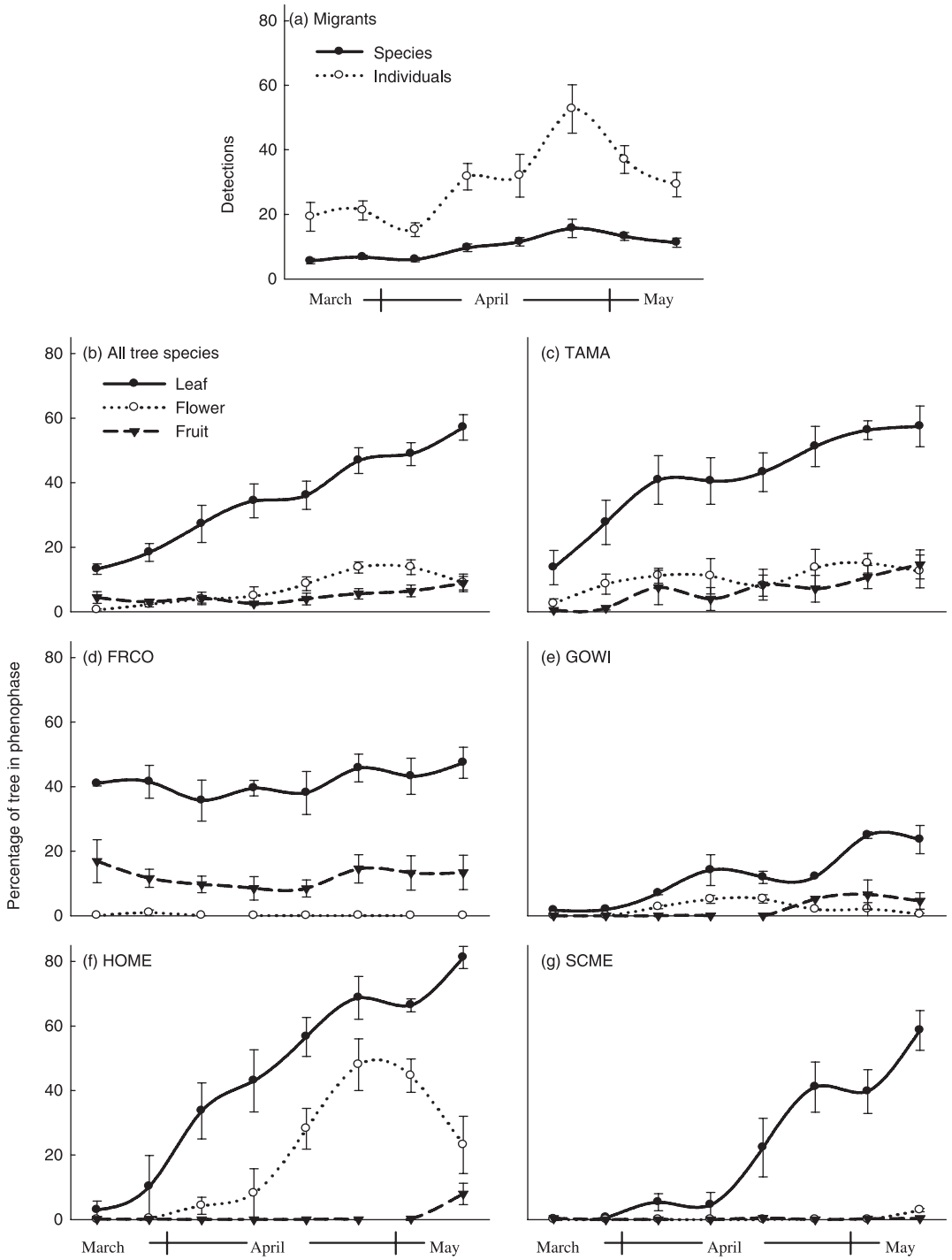

Fig. 1. Tree phenology and migrant diversity and abundance change in concert. Tree species expressed diverse phenological patterns, but generally, leaf, flower, and fruit development were highly correlated (b–g). While migrant diversity and abundance (a) correlated with the average leaf and flower phenology of all tree species (b), only the flowering phenology of honey mesquite (f) predicted migrant diversity and abundance independently. For ease of comparison, graphs present mean phenology and migrant diversity and abundance of eight periods throughout the spring, but analyses were conducted on raw data. Error bars indicate SEM across years.

MICROHABITAT PREFERENCE

To assess microhabitat preferences, we sampled individual birds along the same transects used for point-count sampling and compared the tree species and phenological conditions of migrant foraging locations against the average weekly phenology (see above) and availability of that tree species based on percentage coverage (i.e. use vs. availability). We compared the location of the first-attack manoeuver, as opposed to the location of first detection, because attack manoeuvers specifically identify foraging location, serve as independent observations (Bell, Hejl & Verner 1990), and reduce bias associated with variation in tree architecture, (Sturman 1968;

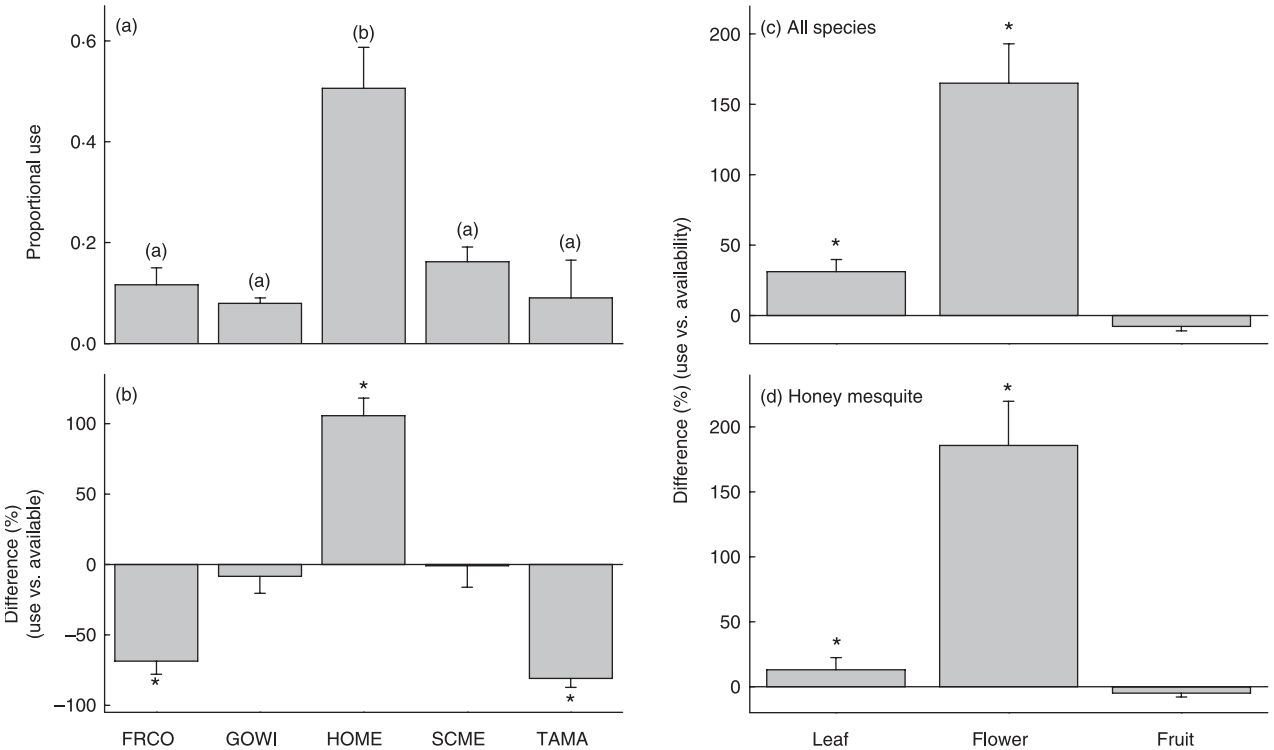

Fig. 2. Migrants prefer honey mesquite with more flowers. Migrants preferentially foraged on honey mesquite over other species (a) and more than expected given their abundance (b). While migrants were more likely to forage on trees with more leaves and flowers (c), only the leaf and flower phenology of honey mesquite predicted microhabitat preferences (d). Responses (b–d) are illustrated by percent preference {[(use-available)/available] × 100} for ease of comparison, but all analyses were conducted on raw data. Columns denoted by different letters are significantly different at the 0·05 level according to an LSD post-hoc test and columns denoted by an asterisk indicate use is significantly different from availability. Error bars indicate SEM across years.

Hertz, Remsen & Zones 1976; Bradley 1985). We tested for differences in tree species preferences using a GLM that included migrant species and year as factors and date as a covariate with least significant difference (LSD) post-hoc tests to identify differences among tree species. We also tested for differences in tree species use vs. availability using a paired *t*-test of the average preferences and availability of each tree species for each sampling period in each year. We examined phenophase preferences for all tree species and each tree species individually using a binary logistic regression, where selected tree vs. nonselected tree was the dependent variable, the three phenophase traits and date were continuous factors, and year and migrant species were included as categorical factors. We excluded nonsignificant interactions from trial models and corrected for multiple tests using a Bonferroni correction.

FOOD AVAILABLITY AND USE

We compared food availability among tree species by sampling branches from the five dominant tree species for arthropods three times in 2003 (April 3, 18; May 6). Branches (1–2·5 cm diameter, 50–70 cm long) were selected within the preferred foraging height of migrants within each tree species (van Riper, unpublished data), and selected branches were removed from the tree, vigorously shaken into a large plastic bag, and visually inspected for hidden arthropods (after Johnson 2000). Because migrants do not forage on all arthropods, we identified preferred species by sampling the diet of a subset of migrants captured by passive mist netting, using a modified lavage technique which has been proven effective in sampling both hard- and soft-bodied arthropods (Moody 1970; Tomback 1975; Rosenberg & Cooper 1990; Poulin, Lefebvre &McNeil 1994). We tested for the influence of tree species and phenology on total arthropod and preferred arthropods abundance using a combination of Pearson correlations and a GLM that included date as a covariate with LSD post-hoc tests to identify differences among tree species. We performed all tests at the lowest taxonomic identification (e.g., morpho-species) and excluded nonsignificant interactions from trial models.

EXPERIMENTAL MANIPULATION OF PHENOLOGY

The timing of leafing, flowering, and fruiting are highly correlated and their relative importance as cues for habitat selection are difficult to discern from observational data alone. For example, in honey mesquite the timing of leafing and flowering often overlap, limiting our ability to identify which cue birds may use to choose foraging locations. To separate among alternative cues, in 2003 we experimentally manipulated the flowering phenology of one of two paired honey mesquite trees. We randomly selected 17 pairs of honey mesquite in full bloom (< 10 m apart) and reduced flower coverage on one, creating two phenology categories: light flower (< 5% coverage) and heavy flower (> 30% coverage). Trees were deflowered by pulling petals by hand, being careful to remove the cue (i.e. the flower), but not the available arthropods, and were continually manipulated throughout the sampling period to maintain light flowering levels.

For each experimental pair, we measured migrant preference by recording the number of birds that visited each tree within a 15-min observation period between sunrise and 09.00 h. We monitored

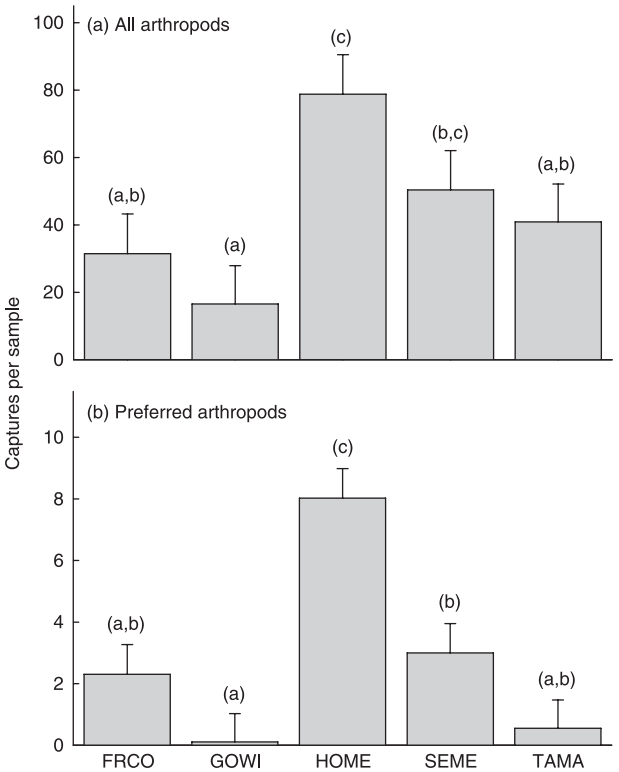

Fig. 3. Food availability is greater on honey mesquite. Total arthropod abundance was greater on honey mesquite, but not significantly (a); however, when only considering preferred foods, arthropod abundance was significantly greater on honey mesquite (b). Columns represent estimated marginal means after controlling for flower phenology. Columns denoted by different letters are significantly different at the 0·05 level according to an LSD post-hoc test.

visitation rate because it indicates a proximate preference for a particular tree type and is known to correlate with food availability (Hutto 1990) enabling us to isolate the effects of removing the settlement cue. Because migrants remain on site for < 48 h (K.L. Paxton, C. van Riper & C. O'Brien, unpublished), we were able to resample experimental pairs every 3 days without fear of pseudoreplication. We tested for the influence of our experimental treatment on flower and leaf phenology as well as migrant visitation using a GLM that included tree pair as factors and date as a covariate. We excluded all nonsignificant interactions from trial models.

Results

MACROHABITAT PREFERENCE

All five tree species expressed unique patterns of phenology, but generally phenological traits were positively correlated (Fig. 1; all leaf-all flower: $\text{Pearson}_{26} = 0{\cdot}809$, $P < 0{\cdot}001$; all leaf-all fruit: $\text{Pearson}_{26} = 0{\cdot}583$, $P = 0{\cdot}002$; all flower-all fruit: $\text{Pearson}_{26} = 0{\cdot}499$, $P = 0{\cdot}009$). Migrant diversity and abundance were positively correlated with the combined flower phenology of all tree species (Fig. 1; diversity: all flower: $F_{1,26} = 13{\cdot}049$, $P = 0{\cdot}02$; date $F_{1,26} = 0{\cdot}035$, $P = 0{\cdot}853$; year: $F_{3,26} = 4{\cdot}693$, $P = 0{\cdot}012$; abundance: all flower: $F_{1,26} = 8{\cdot}024$, $P = 0{\cdot}010$; date $F_{1,26} = 0{\cdot}406$, $P = 0{\cdot}531$; year: $F_{3,26} = 1{\cdot}998$, $P = 0{\cdot}147$). However, when examined independently, only the flowering phenology of honey mesquite correlated with both diversity and abundance of migrants (Fig. 1; diversity: HOME flower: $F_{1,26} = 18{\cdot}447$, $P < 0{\cdot}001$; date $F_{1,26} = 0{\cdot}566$, $P = 0{\cdot}461$; year: $F_{3,26} = 5{\cdot}099$, $P = 0{\cdot}009$; abundance: HOME flower: $F_{1,26} = 9{\cdot}622$, $P = 0{\cdot}006$; date $F_{1,26} = 0{\cdot}085$, $P = 0{\cdot}773$; year: $F_{3,26} = 1{\cdot}916$, $P = 0{\cdot}159$), although the flowering phenology of screwbean mesquite did correlate with diversity (diversity: SCME flower: $F_{1,26} = 13{\cdot}418$, $P = 0{\cdot}002$; date $F_{1,26} = 2{\cdot}131$, $P = 0{\cdot}161$; year: $F_{3,26} = 2{\cdot}741$, $P = 0{\cdot}072$).

MICROHABITAT PREFERENCE

At the microhabitat level, tree species also significantly influenced migrant foraging decisions (tree: $F_{4,20} = 21{\cdot}540$, $P < 0{\cdot}001$; year: $F_{3,20} = 0{\cdot}621$, $P = 0{\cdot}15$), as migrants were found on honey mesquite more than other species (Fig. 2a) and more than availability would predict (Fig. 2b; HOME: $t_3 = 5{\cdot}299$, $P = 0{\cdot}013$; FRCO: $t_3 = -6{\cdot}587$, $P = 0{\cdot}008$; TAMA: $t_3 = -7{\cdot}87$, $P = 0{\cdot}006$). Migrants also preferred trees of all species that had more leaves and flowers (Fig. 2c; all leaf: $\text{Wald}_1 = 28{\cdot}143$, $P < 0{\cdot}001$; all flower: $\text{Wald}_1 = 40{\cdot}254$, $P < 0{\cdot}001$; all fruit: $\text{Wald}_1 = 0{\cdot}914$, $P = 0{\cdot}339$; year: $\text{Wald}_1 = 4{\cdot}426$, $P = 0{\cdot}035$; date: $\text{Wald}_1 = 16{\cdot}748$, $P < 0{\cdot}001$; tree species: $\text{Wald}_4 = 20{\cdot}502$, $P < 0{\cdot}001$; migrant species: $\text{Wald}_{13} = 5{\cdot}253$, $P = 0{\cdot}969$), but similar to macrohabitat patterns, when examined independently, only the phenology of honey mesquite was positively correlated with microhabitat preferences (Fig. 2d; HOME leaf: $\text{Wald}_1 = 14{\cdot}598$, $P < 0{\cdot}001$; HOME flower: $\text{Wald}_1 = 16{\cdot}599$, $P < 0{\cdot}001$; HOME fruit: $\text{Wald}_1 = 1{\cdot}441$, $P = 0{\cdot}230$; year: $\text{Wald}_1 = 0{\cdot}772$, $P = 0{\cdot}380$; date: $\text{Wald}_1 = 6{\cdot}320$, $P = 0{\cdot}012$; migrant species: $\text{Wald}_{11} = 0{\cdot}781$, $P = 1{\cdot}000$).

FOOD AVAILABLITY AND USE

We collected 172 different morpho-species representing 12 orders; however, migrant stomach contents included only nine orders of which five morph-species (preferred arthropods) made up > 25% of their total diet. Tree species (Fig. 3) and phenology (Fig. 4) influenced both total (tree species: $F_{4,309} = 3{\cdot}514$, $P = 0{\cdot}008$; leaf: $_{1,309} = 1{\cdot}311$, $P = 0{\cdot}253$; flower: $F_{1,309} = 61{\cdot}274$, $P < 0{\cdot}001$) and preferred arthropod abundance (tree species: $F_{4,309} = 5{\cdot}962$, $P < 0{\cdot}001$; leaf: $_{1,309} = 2{\cdot}757$, $P = 0{\cdot}098$; flower: $F_{1,309} = 50{\cdot}139$, $P < 0{\cdot}001$); however, only preferred arthropod abundance differed between tree species (Fig. 3b). When examined independently, total arthropod abundance was positively correlated with the flowering phenology of three of the five tree species (HOME flower: $F_{1,70} = 18{\cdot}549$, $P < 0{\cdot}001$; GOWI flower: $F_{1,59} = 30{\cdot}929$, $P < 0{\cdot}001$; TAMA flower: $F_{3,60} = 21{\cdot}771$, $P < 0{\cdot}001$), but preferred arthropod abundance was only correlated with the flowering phenology of honey mesquite (Fig. 4d; HOME flower: $F_{1,70} = 30{\cdot}752$, $P < 0{\cdot}001$).

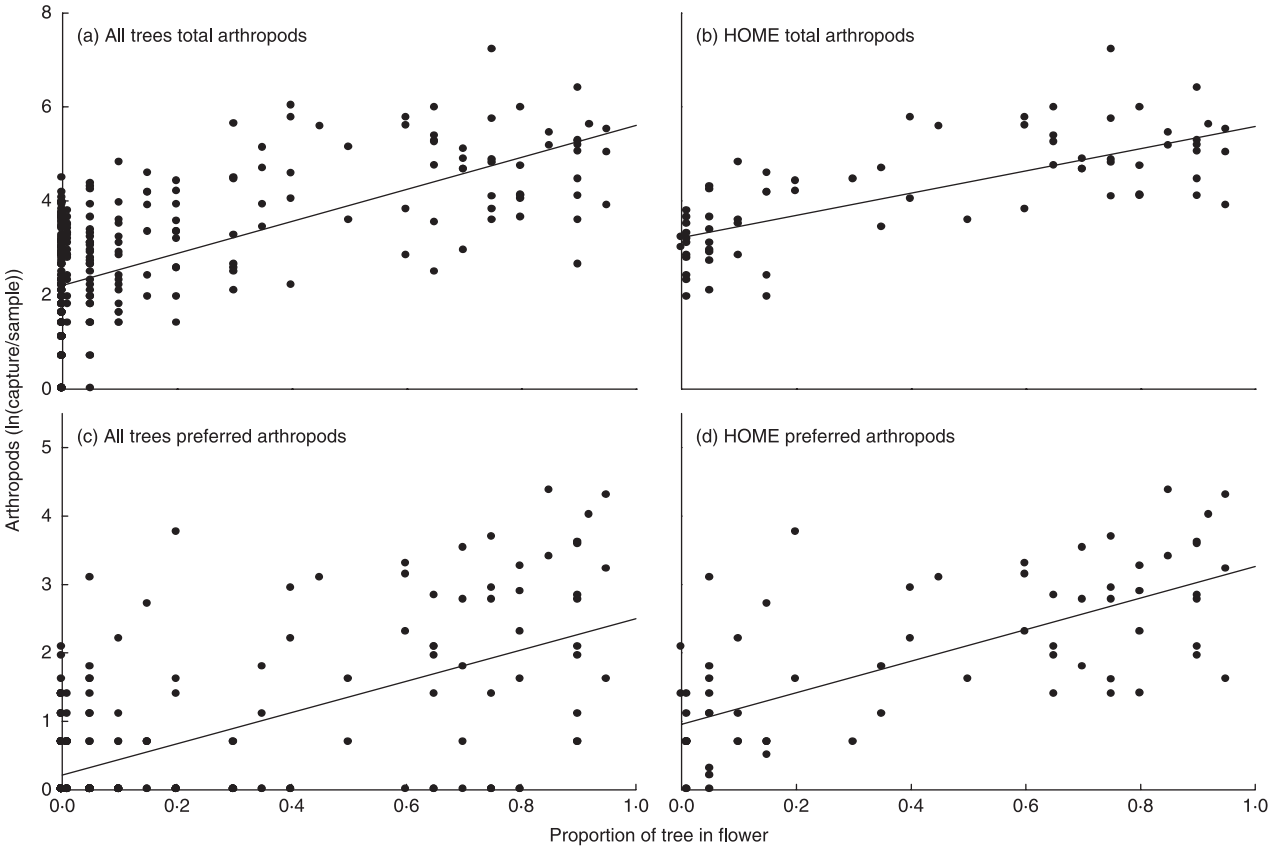

Fig. 4. Food availability increases with flower coverage. While total arthropod abundance (a) and preferred arthropod abundance (c) correlated with the average flower phenology of all tree species (b), only the flowering phenology of honey mesquite (b, d) predicted both total and preferred arthropod abundance independently. For ease of comparison, arthropod abundance is presented as ln(capture/sample), but all analyses were conducted on raw data.

EXPERIMENTAL MANIPULATION OF PHENOLOGY

Experimental manipulations significantly reduced flower coverage (Fig. 5a; treatment: $F_{1,128} = 530{\cdot}226$, $P < 0{\cdot}001$; tree pair: $F_{16,128} = 2{\cdot}430$, $P = 0{\cdot}004$; date: $F_{1,128} = 14{\cdot}231$, $P < 0{\cdot}001$), but not leaves (Fig. 5a; treatment: $F_{1,128} = 1{\cdot}253$, $P = 0{\cdot}265$; tree pair: $F_{16,128} = 4{\cdot}015$, $P < 0{\cdot}001$; date: $F_{1,128} = 91{\cdot}801$, $P < 0{\cdot}001$) and resulted in a significant decrease in visitation rate of migrants (Fig. 5b; treatment: $F_{1,128} = 28{\cdot}094$, $P < 0{\cdot}001$; tree pair: $F_{16,128} = 1{\cdot}757$, $P = 0{\cdot}047$; date: $F_{1,128} = 2{\cdot}142$, $P = 0{\cdot}146$).

Discussion

Migration is an important component of the life history of migratory birds, and for species that do not migrate continuously, where they stop to rest and refuel can have important implications for future survival and reproduction (Piersma 1990; Moore *et al*. 1995, 2005; Petit 2000). Yet, despite the importance of stopover decisions to avian life-history evolution and migratory bird conservation, we know little about how birds select stopover habitats. Predation and competition may shape stopover decisions, but food availability likely determines habitat preference (Hutto 1985a; Petit 2000; Moore *et al.* 2005). Birds are sensitive to food availability (Morris *et al.* 1958; MacArthur & Pianka 1966; Zach & Falls 1976) and can preferentially settle in food-rich environments (e.g. Hutto 1980; Yard *et al.* 2004); yet, the cues underlying these decisions remain unclear. Using both observational and experimental evidence, we show for the first time that the flowering phenology of a common tree species, honey mesquite, acts as a reliable settlement cue for insectivorous Neotropical migrant birds at both the macro- and micro-habitat levels.

Although we examined the phenology of all five major tree species along the Lower Colorado River, only the flowering phenology of honey mesquite consistently predicted seasonal variation in migrant diversity and abundance (Fig. 1). Mesquite flowers are highly visible and therefore may reduce search time in unfamiliar habitats. Furthermore, total and preferred arthropod abundance correlated with the flowering phenology of honey mesquite (Fig. 4), indicating the reliability of flowers as a settlement cue and implying that migratory timing and routes may have evolved to exploit this readily available and explicitly advertised resource. Indeed, exploitation of high elevation and monsoon-dependent habitats by fall migrant populations (e.g. DeLong, Cox & Cox 2005) suggests that stopover habitat preferences may be highly dependent upon area phenology. Alternatively, since

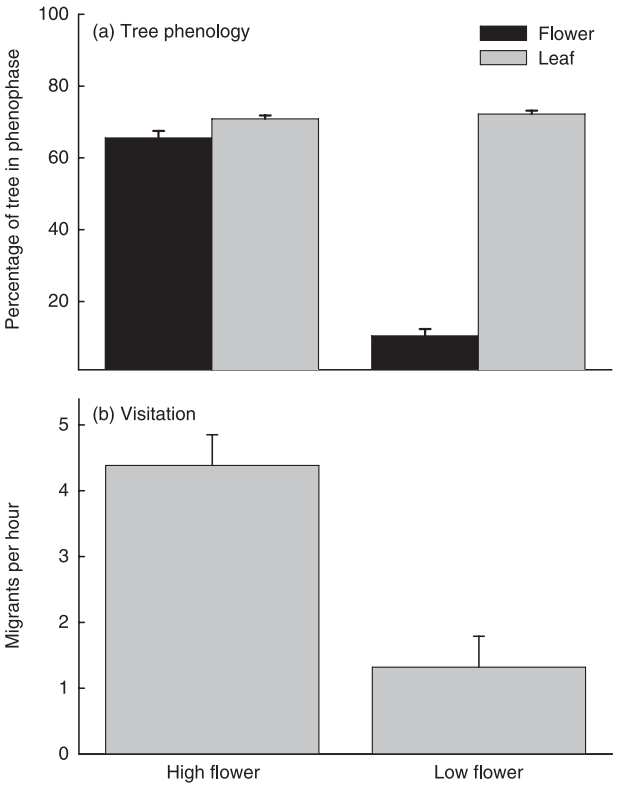

Fig. 5. Migrant visitation reflects differences in flower cues. Flower manipulation significantly altered flowering, but not leaf phenology (a), and resulted in reduced visitation by migrants (b). Columns represent estimated marginal means with standard errors after controlling for date.

arthropod herbivory and the production of chemical defenses to combat herbivory, represent significant costs (Agren & Schemske 1993; Agrawal, Strauss & Stout 1999), the phenology of honey mesquite may have evolved to exploit migrants as a natural insecticide (e.g. Marquis & Whelan 1994). Indeed, birds may significantly reduce the costs of arthropod herbivory, increasing survival and reproduction of host plants (reviewed in Schmitz, Hambäck & Beckerman 2000). That honey mesquite had the greatest abundance of arthropods (Fig. 3), and > 25% of the diet of migrants consisted of herbivorous insects, suggests such a possibility. The extreme abundance and concentration of migrants during spring migration may create a positive feedback loop whereby migrants reduce the costs of herbivory enabling honey mesquite trees to invest more in reproduction, producing more flowers, and thus a stronger signal to attract more migrants. In either case, the close tie between the timing and distribution of Neotropical migrants and the flowering phenology of honey mesquite suggests a strong co-evolutionary relationship.

Similar to the macrohabitat patterns, migrants preferred honey mesquite to other tree species, and particularly honey mesquite with more flowers (Fig. 2). That migrants prefer trees with more flowers (Fig. 2) is not surprising given the greater availability of food (Fig. 4); indeed, there are many empirical studies demonstrating the ability of birds to track food availability (Morris *et al.* 1958; Hildén 1965; MacArthur & Pianka 1966; Zach & Falls 1976; Hutto 1980, 1981, 1985b; Yard *et al.* 2004). Surprisingly, experimental tests of the importance of food availability in stopover decisions have failed to find a causal relationship (e.g. Hutto 1990); however, our data suggest an important distinction. Previous experiments altered food availability without changing the proximate cues birds rely upon to select appropriate habitats (Hutto 1990). Here we directly manipulated one settlement cue, flower phenology, and show migrants prefer honey mesquite trees with more flowers independent of other vegetative cues (Fig. 5) or actual food availability. Alternatively, by manipulating flower abundance, we may have inadvertently reduced arthropod abundance, leading to changes in migrant habitat preferences based on food availability and not flower phenology; however, this is unlikely. First, although flower availability likely influences the distribution of pollinating arthropods, a minor component of migrant diet, herbivorous arthropod are more dependent on leaf phenology (e.g. Murakami *et al.* 2007), which was unchanged (Fig. 5a). Second, migrants primarily persist on small cryptic arthropods, thus even if we did alter food availability, it is unlikely that birds could directly assess differences before visiting each tree. Indeed, the failure of previous studies to affect migrant habitat preferences by altering food availability (e.g. Hutto 1990) may reflect the importance of arthropod behaviours in determining which cues birds use to select stopover locations. Still, any accidental change to arthropod abundance may have been advertised via public information (e.g. Doligez *et al*. 2004), but given that migrants tended to arrive and forage alone suggests otherwise, and highlights the potential importance of vegetative cues in selecting foraging locations.

Conclusion

In the western USA, Neotropical migrants and their riparian migratory corridors are topics of conservation concern (Heglund & Skagen 2005; van Andel & Aronson 2006); yet little is known about the factors limiting migratory bird populations, particularly as it pertains to the ecology of migration. Given the strong correlation between honey mesquite flowering phenology and migrant populations at the macrohabitat level, as well as experimental and observational evidence of preference for flowering honey mesquite at the microhabitat level, it appears that the flowering phenology of honey mesquite is an important settlement cue for Neotropical migrant birds. That the flowering phenology of honey mesquite is a reliable indicator of food availability indicates the importance of this cue for migrant populations, at least along the Colorado River. It remains unclear how the phenology of honey mesquite or other tree species may influence migratory behaviours along other important migratory corridors that differ geographically, have different migratory peaks, and support different population and species assemblages (Skagen *et al.* 2005; Paxton *et al.* 2007). Furthermore, preferences based on proximate vegetative cues that likely

respond independently from ultimate selective pressures acting on migratory timing or food availability, highlight the potential for this system to transform into an ecological trap (Robertson & Hutto 2006). Future research should focus on the generality of flowering phenology as a settlement cue and how anthropogenic change, such as climate change and invasion by exotic tree species, may alter flower cues, migrant preference, and food availability independently to impact migrant populations.

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